The use of phytoliths as a proxy for distinguishing ecological communities: A preliminary phytolith reference collection for the mountains of Dhufar, Oman

Undergraduate Research Thesis

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Abstract:

The Dhufar Mountains region of Oman has high ecological diversity, circumscribed by distinct landscape zones, largely due to the effect of waning summer monsoon cloud precipitation. The Ancient Socio-Ecological Systems in Oman (ASOM) project uses a coupled human and natural systems approach to study the emergence of territoriality in pastoralist systems in Dhufar using a multitude of datasets and proxies. One such proxy are phytoliths, silicon dioxide microfossils formed in the cellular and intercellular spaces of living vascular plants. These sediment components remain in soils following the death and decay of above-ground plant tissue and as a result can be used in the study of past vegetation community dynamics. Due to uneven rates of phytolith formation based on plant family and small potential for post-burial contamination, it is best to document phytoliths at the community-level. My study addressed the differences in phytolith morphotypes and densities of the tallgrass savannah and inner-Nejd plant communities of Dhufar, two communities that reflect variation in vegetation structure and composition. For robust analysis, I created a reference collection of these two communities to detect possible morphotypes indicative of specific taxa and differences in phytolith production. To reduce the total sample set to the most meaningful types, I selected among all plants identified in botanical surveys by two criteria: 1) those most indicative of the circumscribed zones according to multiple classifications, and 2) high phytolith producing potential. Phytoliths were extracted from the leaves of each specimen via dry-ashing and phytolith densities and morphotypes were then assessed by counting under a microscope. The results indicated that phytolith density was not a distinguishing characteristic between the tallgrass savannah and the inner-Nejd zone, but that the number of phytolith types produced by each community was significantly different. Many trends in lobate abundance and bar length in characteristic panicoid grasses matched those found in the literature: *Themeda quadrivalvis* and *Setaria pumila* produced bilobe phytoliths with longer bar lengths in general, whereas *Apluda mutica* produced a high ratio of polylobes and shorter bilobe phytoliths in comparison to the other two taxa. With little work done on phytoliths from the Southern Arabian highland region, this study presents an introduction to their use as a paleoecological proxy for understanding the ecologies and vegetation communities of the region.

Introduction:

The objective of this study was to determine whether phytolith morphotypes and densities are robust criteria for discriminating vegetation cover in the various ecological communities of Dhufar, Oman. This was accomplished by first expanding an herbarium reference collection of the various indicator species of ecosystems found throughout the landscape. Many studies have surveyed the distinct vegetative communities of Dhufar and the Southern Arabian highlands (Miller and Morris, 1988; Kurschner *et al*., 2004; Kurschner *et al*., 2008, Mosti *et al*., 2012; Patzelt, 2015), but limited phytolith analysis and reference material exist for the plants of the region (Ball *et al*., 2002). Thus, I aimed to contribute to the growing knowledge of phytolith work and make steps towards establishing a phytolith reference collection specific to the characteristic plants within the mountains and north-flowing wadis of Dhufar.

Secondly, analysis of phytolith density and morphology would reveal whether distinctions could be made between and within the various plant communities under consideration. This study examined the vegetation overlap between the tallgrass savannah and the southern, or inner, region of the Nejd. These two communities form an ecological transition zone of potential significance due to modern degradation, overgrazing, and shifts in climate (Hildebrandt and Eltahir, 2006). Previous research shows that phytolith abundance in monocotyledons, such as grasses, is considerably greater on average than in dicotyledons (Albert and Weiner, 2001). An experimental study I conducted on two taxa from these communities confirmed this difference for my dataset (Buffington *et al*., forthcoming). Furthermore, lobate phytoliths, indicative of panicoid grasses and tallgrass prairie communities, may demonstrate distinctiveness in sub-morphotypes between certain grass taxa (Ball *et al*., 2002; Lu and Liu, 2003). Here I tested whether the tallgrass and inner-Nejd communities could be differentiated by phytolith density and the number of phytolith types produced. Furthermore, I calculated lobate ratios for the three panicoid grasses of the tallgrass community based on bar length. The findings of my study ultimately provide a foundational framework for the use of phytoliths as an environmental proxy in reconstructing vegetative and palaeoclimatic datasets of Dhufar.

Background:

ASOM Project and Implications

Gaining a deeper understanding of the human-environment dynamics in the past can provide insight into what factors shape a society. The archaeology of Southern Arabia has suggested long-term and dynamic couplings between ecological and social processes that influence the mobility and settlement of pastoralists (McCorriston *et al*., 2011; 2014). Broadly, the Ancient Socioecological Systems in Oman (ASOM) project uses archaeological, ecological, and agent-based modeling datasets to study whether and how the environment influences patterns of human territoriality and how territoriality in turn influences the environment. Methods of surveying, mapping, and excavating human habitation sites and paleoecological features allow for the collection of soils and proxies to reconstruct ancient environments and shifts in vegetation and climate overtime. Furthermore, pastoral decisions on mobility, settlement, and territoriality are largely based on seasonal shifts in water and grazing resource availability (Roe *et al*., 1998). Thus, phytoliths as a proxy for localized vegetation can be valuable for documenting past resource availability which is crucial for pastoral decision-making. Such analyses may also serve as a basis from which to develop sustainable and practical management techniques for modern rangeland and pastoral environments in the future.

Dhufar Ecology

Dhufar is an excellent arena for examining the development of natural and anthropogenic landscapes due to long-term human occupation, a consistent pastoral economy, and because the region is ecologically unique owing to the waning summer monsoon cloud precipitation (Miller and Morris, 1988; Hildebrandt and Eltahir, 2006; Fleitmann *et al*., 2007). The region is divided into four adjoined biogeographical units that reflect remarkably circumscribed vegetation, which regional environmental proxies suggest has been stable since the mid-Holocene (Fleitmann *et al*., 2007; Cremaschi and Negrino, 2005). First, the *Acacia-Commiphora* open shrubland dominates the coastal plain and south-facing slopes towards the Arabian Sea (Patzelt, 2015). North of the coastal plain is the *Anogeissus dhofarica* forest of the escarpment zone, a rich plant community heavily influenced by the monsoonal fog oasis. Genetic diversity analyses suggest that the *Anogeissus dhofarica* forest is a remnant patch of a previously continuous forest belt of palaeo-

African origin (Kurschner *et al*, 2004; Oberprieler *et al*, 2009; Patzelt, 2015). Northward, the *Themeda quadrivalvis* tallgrass savannah of the plateau replaces the *Anogeissus* forest. This grassland community is comprised primarily of grasses representative of a species-deficient version of the East African savannah (Patzelt, 2011). Finally, the Nejd consists of sparsely scattered trees, shrubs, and grasses throughout many large wadi systems that are residually affected by monsoon precipitation and receive little rain (Patzelt, 2015).

Palaeoclimatic reconstructions of precipitation, such as those based on speleothems, suggest a significant shift towards aridity at roughly 5500 BP, at the initiation of the mid-Holocene. This drying trend may have been buffered in the mountains and wadis of Dhufar's South Arabian highlands, a landscape long impacted by human and animal use (Fleitmann *et al*., 2007). Rainfall is an important factor, but it is not the only one determining the vegetation structure of a given location. The wet season in Dhufar today, locally known as the *Khareef*, lasts for roughly three months in the summer (June – September) and is accompanied by orographic clouds whose moisture is captured by the forest canopy for long-term growth and survival (Hildebrandt and Eltahir, 2006). Ecological modeling evidence suggests that such horizontal precipitation plays a significant role in sustaining this unique ecological niche and that modern degradation and overgrazing, as well as decreased cloud cover, soil absorption, and root depth, can lead to possible forest extinction in favor of an extended grassland ecosystem (Hildebrandt and Eltahir, 2006; 2007). Detailed paleobotanical analyses of the tallgrass-Nejd transition zone in the past may provide important insight into the shifting plant assemblages of Dhufar as they respond to changes in hydrology, climate, and human use of the land.

Phytoliths as an Environmental Proxy

Initially amorphous silica gels absorbed by plants from groundwater, phytoliths are formed when silica is laid down as silicon dioxide (SiO_2) bodies in the cellular and intracellular spaces of living plant tissue. These silica bodies reflect diagnostic cellular structures, which in turn may reflect many vegetation classes of interest (Piperno, 2006). While proxies such as carbonates and pollen allow us to reconstruct regional climates over thousands of years, phytoliths reflect highly localized vegetation, are durable under a wide range of soil conditions, and persist in the soil even after the plant has decayed (Piperno, 2006). Spatially and temporally

discrete phytolith assemblages offer proxies for former plant cover and landscape dynamics (Piperno, 2006; Rosen and Weiner, 1994).

A phytolith reference collection is crucial for positive identification of indicator phytoliths. Ball *et al*. (2002) published the results of a modern reference collection focusing on the vegetation of Dhufar's coastal plains and south-draining wadis. Recently, some of these associations and phytolith identifications have been published on the PhytCore database. However, these regions reflect a potentially different vegetation composition than the vegetation of Dhufar's mountains and northward flowing wadis. Other than Ball's study, our archaeobotany laboratory only has access to broader Arabian Peninsula taxa references from Professor Arlene Rosen's collection (Israel/Jordan) and derived from Professor Joy McCorriston's research in Syria, Jordan, and Yemen (McCorriston, unpublished data). My study contributed to this gap in reference material by collecting characteristic taxa to add to the existing phytolith reference slides.

Phytolith production and diagnostic capability varies considerably from plant to plant. Piperno (2006: pp. 7) conducted a thorough synthesis of previous phytolith studies to devise a classification system based on plant family. A Tier 1 classification represents families for which phytolith density and production are usually high and phytoliths distinctive to subfamily and genus are common. A Tier 2 classification represents families for which phytolith production may not be high in some species, but family and genus-specific types can occur. A Tier 3 classification represents families for which phytolith production may be common in some genera, but distinctive forms are limited. A Tier 4 classification represents families for which phytolith production is variable among subfamilies and distinctive forms are limited. A Tier 5 classification represents families for which phytolith production is uncommon and forms show no taxonomic significance. I used this tier system in my study as a criterion for selecting priority Tier 1 taxa to collect and extract phytoliths.

Of the Tier 1 plant families, Poaceae (Gramineae), or the grasses, are often of special interest for phytolith analyses. Many grasses demonstrate high levels of phytolith production and produce morphotypes that are specific to subfamily (Piperno, 2006). Grass short cell phytoliths such as rondels and towers are highly diagnostic types of the Pooideae subfamily and C_3 grasses; saddles are highly diagnostic of the Chloridoideae subfamily and C_4 shortgrass prairies; and bilobes, polylobes, and cross bodies are largely considered representatives of the Panicoideae

subfamily and C_4 tallgrass prairies (Twiss, 1992). Previous research on phytoliths from southern Oman suggests that several grass taxa reflect bilobe phytoliths with distinctive properties, but such distinctions were not examined in detail (Ball *et al*., 2002; Lu and Liu, 2003). Furthermore, monocotyledon plants have consistently produced higher densities of phytoliths compared to dicotyledons (Albert and Weiner, 2001; Piperno, 2006). The potential to distinguish taxa based on attributes such as diagnostic types, phytolith density, and bilobe sub-types is significant for evaluating the structure and composition of a community's vegetation over time.

Because phytoliths form at uneven rates in different plant families, their use as a paleoecological proxy is therefore best understood by first examining morphotypes distinct to certain taxa and ecologies at the community level. After establishing references for phytolith density and type, comparisons of soil-based phytolith assemblages and resultant environmental indices may then reveal differences in regional environmental structure, stability, and depositional materials (Twiss, 1992; Fredlund and Tieszen, 1994; Alexandre *et al.*, 1997; Albert and Weiner, 2001). Powers *et al*. (1989) demonstrated that even a conservative, simple assemblage of phytolith shapes can be used to differentiate between windblown sands and cultivation deposits, peat, and fecal remains found in phytolith assemblages of northwest Britain. Using leaf reference samples rather than sediments containing phytoliths from unknown taxa, my study advanced this morphotype-comparison approach by distinguishing 1) phytoliths from families of various tier classifications, 2) phytolith densities and types from two ecological communities, and 3) bilobe phytoliths sub-classified by bar length.

Hypotheses:

The null hypothesis of my study was that the communities are not differentiated by phytolith density nor number of types. I tested whether or not the tallgrass and inner-Nejd communities could be differentiated based on phytolith density (Hypothesis 1 [H1]) and the number of phytolith types produced (Hypothesis 2 [H2]). Finally, I tested the hypothesis that the lobate phytolith ratios are specific taxa (Hypothesis 3 [H3]).

Materials and Methods:

Priority Taxa and Field Collection:

Mosti *et al*. (2012)'s floristic list of plants collected in discrete locations throughout Dhufar served as a foundational inventory of the species needed for the phytolith reference collection. The collection sites in Mosti *et al.* (2012) were classified by ecology and altitude. I first sorted through the list to determine which of the collection sites were located in the north flowing wadis, mountain slopes and grasslands, or high hills and grasslands because these locations reflect a high number of distinct plant communities in Dhufar. Next, nine of Mosti *et al.'s* (2012) survey locations were selected as the closest and most relevant to the ASOM project study sites based on ecological and vegetative similarities (Fig. 1). Taxa observed and reported at these nine sites (Mosti *et al.,* 2012) were then prioritized for collection based on indication of ecological community (Kurschner *et al*., 2004; Patzelt, 2015; Miller and Morris, 1988) and phytolith production and diagnostic potential via the phytolith tier system (Piperno, 2006).

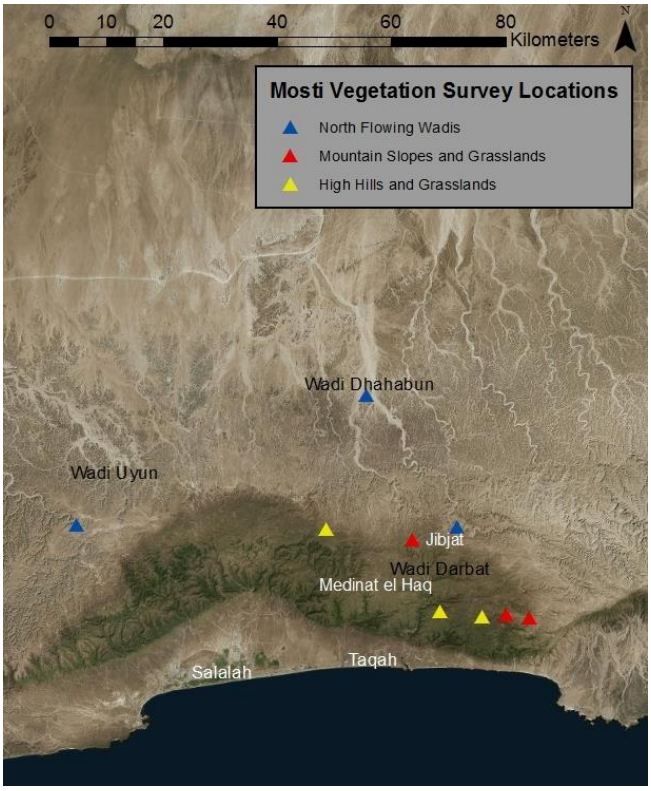

Figure 1: Map of locations surveyed by Mosti *et al.* (2012) in the mountains of Dhufar that coincide ecologically and botanically with my survey sites of interest

I traveled to Oman from October 5-21, 2018 with support from the National Science Foundation (NSF) grant of the ASOM project and under the guidance of Professor Joy McCorriston and Abigail Buffington. I collected thirty-nine characteristic species representing the various plant communities of the mountains of Dhufar. Leaf materials from eighteen species were sampled from the nursery of the Oman Botanic Garden in Muscat, Oman. These samples were collected with shears which were washed between cuttings with distilled water and placed into paper envelopes. Additionally, one sample was collected from the Oman Botanic Garden herbarium. Nine species were collected in Dhufar during botanical field surveys in October 2018. These samples were taken directly from the field and placed into paper envelopes. The remaining eleven samples were collected from herbarium specimens housed in the National Herbarium maintained by Azzah al Jabri in the Natural History Museum in Muscat, Oman and the Near Eastern Archaeology and Archaeobotany Laboratory (NEAAL) herbarium of Professor Joy McCorriston at The Ohio State University in Columbus, Ohio. Specimens collected from the nursery and the field were dried and pressed before being shipped to The Ohio State University, under permits from the Oman Botanic Garden and the United States Department of Agriculture (USDA), for laboratory analysis.

Focal Communities

For the purpose of this study, I investigated the tallgrass savannah and the inner-Nejd plant communities because they reflect distinct variation in floral structure (Patzelt, 2015) and contain multiple taxa classified as Tier 1 phytolith producers (Table 1). The tallgrass community also consists of more monocotyledon species than the inner-Nejd community and should therefore be differentiated from the inner-Nejd community based on phytolith density. Lastly, these two communities form a transition zone of potential significance due to modern degradation and overgrazing (Hildebrandt and Eltahir, 2006).

The tallgrass savannah is low in species diversity and covers much of the plateaus and montane zones of Dhufar (Fig. 2). Characteristic plant species of this community include *Themeda quadrivalvis, Setaria pumila, Apluda mutica, Abelmoschus manihot* (Patzelt, 2015: pp 305), and the common grazing indicator *Achyranthes aspera* (Kürschner, 2004: pp. 583). Although these taxa are representative of the tallgrass savannah, they are also found in other ecological zones such as the escarpment and coastal plain. Next, the inner-Nejd plant community

is dominated by small shrubs and grasses and occupies the montane and high-montane zones of the region (Fig. 2). The common frankincense tree, *Boswellia sacra*, as well as *Tetraena decumbens*, *Trichodesma cinereum*, and *Euphorbia orbiculifolia* can all be found within the wadis of this region (Patzelt, 2015: pp. 309). *Commiphora gileadensis* is also a characteristic species of the inner Nejd and is especially prevalent in the *Euphorbia-Commiphora* community favoring rocky surfaces at high altitudes (Patzelt, 2015: pp. 306).

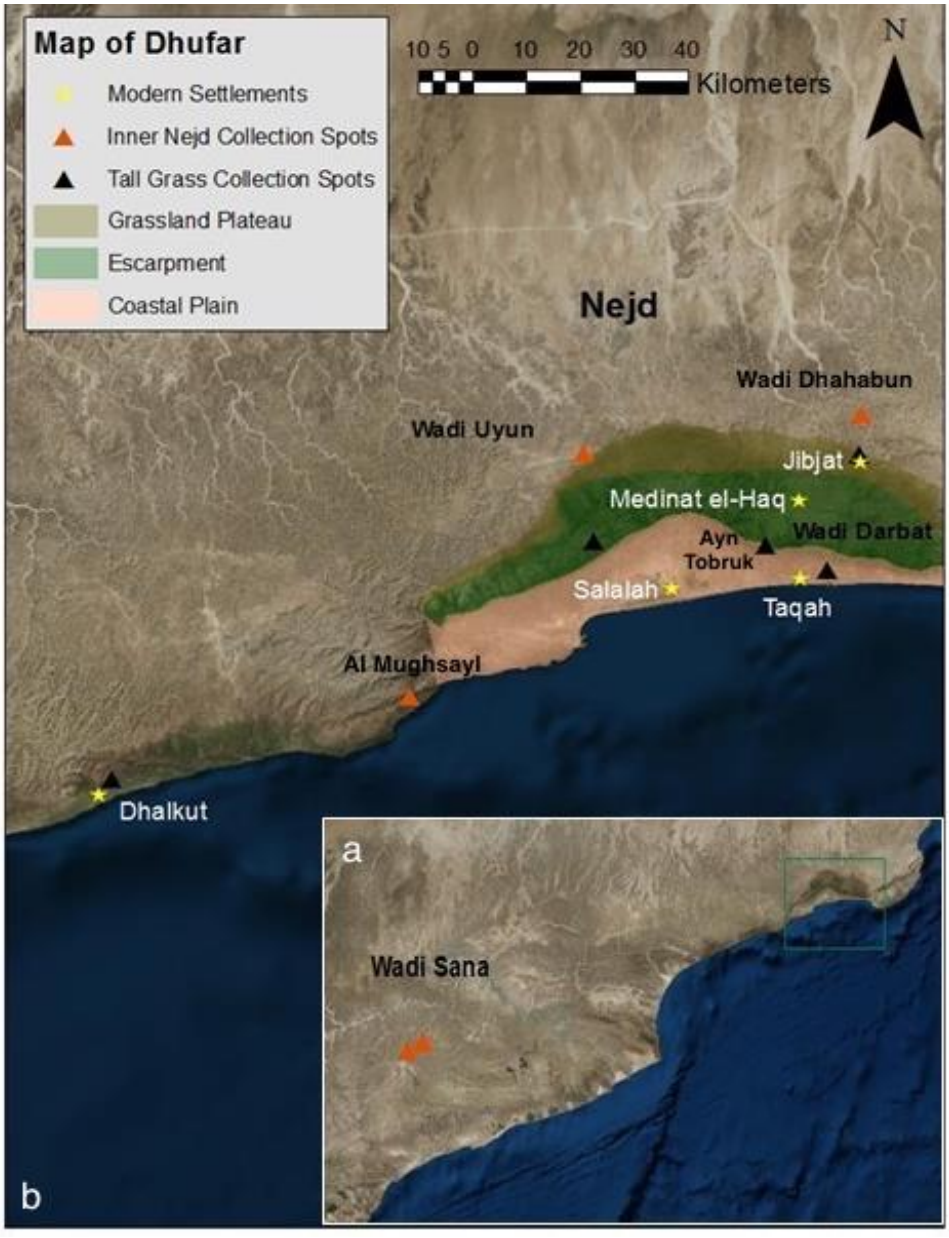

Figure 2: Map of collection locations in the South Arabian highland region (a) and the Dhufar mountains region (b) for the samples used in this study

Table 1: Taxa collected for phytolith analysis

Family	Taxa	Tier	Ecological Zone	Habit	Collection Coordinates
Burseraceae	*Commiphora gileadensis*	1	*Inner-Nejd*	Shrub or small tree	15° 47’ 03” N 049° 28’ 28” E
Burseraceae	*Boswellia sacra*	1	*Inner-Nejd*	Tree	15° 40’ 02” N 049° 17’ 23.8” E
Boraginaceae	*Trichodesma cinereum*	1	*Inner-Nejd*	Herbaceous	17° 18’ 59.7” N 054° 29’ 57.3” E
Euphorbiaceae	*Euphorbia orbiculifolia*	2	*Inner-Nejd*	Bulb	16° 50’ 64” N 053° 41’ 65” E
Zygophyllaceae	*Tetraena decumbens*	5	*Inner-Nejd*	Small shrub	17° 15’ 35.8” N 054° 00’ 50.0” E
Poaceae (Gramineae)	*Themeda quadrivalvis*	1	Tallgrass	Grass	17° 05’ 51” N 054° 19’ 34” E
Poaceae (Gramineae)	*Setaria pumila*	1	Tallgrass	Grass	16° 42’ 59” N 053° 11’ 08” E
Poaceae (Gramineae)	*Apluda mutica*	1	Tallgrass	Grass	17° 15’ 20.1” N 054° 29’ 30.72’ E
Malvaceae	*Abelmoschus manihot*	4	Tallgrass	Herbaceous	17° 06’ 41.1” N 054° 01’ 45.7” E
Amaranthaceae	*Achyranthes aspera*	5	Tallgrass	Herbaceous	17° 03’ 16” N 054° 25’ 60” E

Provenience of Focal Community Materials:

I collected four of the samples used in this study in October 2018 during botanical field surveys with the help of Dr. Annette Patzelt (Director, Oman Botanic Garden, Muscat, Oman), Andrew Anderson, (Senior Landscape Architect, Oman Botanic Garden, Muscat, Oman), and Tony Miller (Director, Centre for Middle Eastern Plants, Royal Botanic Garden, Edinburgh, UK). *Apluda mutica* was collected next to the enclosed area just outside Jibjat. *Abelmoschus manihot* and *Tetraena decumbens* were collected alongside the road to Wadi Uyun, and

Trichodesma cinereum was collected in Wadi Dhahabun. Four specimens were sampled by Abigail Buffington at the National Herbarium in the Natural History Museum in Muscat, Oman. *Themeda quadrivalvis* was collected on 27 Sep 1992 by I. McLeish near Ayn Tobruk. *Euphorbia orbiculifolia* was collected on 10 Sep 2002 by M. Raffaelli, M. Tardelli, and S. Mosti alongside the coastal road beyond Al Mughsayl. *Achyranthes aspera* was collected on 1 Sep 2002 by M. Raffaelli, M. Tardelli, and S. Mosti alongside the road from Salalah to Wadi Darbat east of Taqah, roughly 2-3 kilometers from the ancient archaeological site of Sumhuram. *Setaria pumila* was collected on 8 Oct 2003 by Annette Patzelt just north of Dhalkut. I sampled the remaining two specimens from Dr. McCorriston's herbarium collection. Both the *Boswellia sacra* and the *Commiphora gileadensis* were collected by Catherine Heyne for the Roots of Agriculture in Southern Arabia (RASA) project in the Wadi Sana region of Yemen. See Figure 2a for collection locations in the South Arabian highlands and Figure 2b for the collection locations in Dhufar.

Laboratory Methods:

Phytolith analysis was conducted for the ten indicator taxa of the inner-Nejd and the tallgrass savannah communities (Table 1). The protocol for extracting phytoliths from dried and herbarium specimen comes from the dry-ashing technique described by Parr (2001). For each taxon sampled, approximately 0.2g of leaf material was rinsed with distilled water and placed in a crucible before ashing in the muffle furnace for eight hours at 500°C. The samples were transferred to a 15-ml centrifuge tube, and 10 ml of 10% hydrochloric acid (HCl) was added. The centrifuge tube was placed in a hot water bath at approximately 70°C for twenty minutes before centrifuging for five minutes at 3500 rpm and decanting. The material that remained was rinsed with distilled water and centrifuged again for five minutes at 3500 rpm and decanted. This process was repeated using 10 ml of 15% hydrogen peroxide (H_2O_2) and a final rinse with distilled water followed. The final remains in the centrifuge tube were transferred to a 50-ml beaker using distill water and a glass pipette and then allowed to dry in a drying oven. Once dry, 1 ml of 100% ethanol (EtOH) was added to the beaker and left to dry overnight. The extracted material was then weighed and mounted onto a glass slide with Entellan mounting material.

The phytoliths on the dried slide were counted under a microscope at 400x by beginning at the top-right corner of the slide and moving down a column transect (Albert and Weiner, 2001). I identified and recorded the different phytolith types present until no new types were

found and then counted one additional column to ensure a representative assortment. I continued counting by column and kept tally marks for each phytolith present until a maximum of 300 phytoliths was reached. I also recorded the total number of fields counted (each view in the microscope displays two fields). Phytolith types were cross-referenced with additional reference material (ArcheoScience PhytCore Database) and unidentifiable morphotypes were photographed for future analyses and interpretation. Additionally, the bar and lobe length measurements and classification system of Lu and Liu (2003: pp. 79) (Fig. 3) were used to distinguish different types of bilobes in the panicoid grasses. In this study, I qualitatively classified the lobate phytoliths into four types based on bar length (Fig. 4a) and general morphology: Type 1 bilobe (Fig. 4b), Type 2 bilobe (Fig. 4c), Type 3 bilobe (Fig. 4d), polylobe (Fig. 4e). While counting *Themeda quadrivalvis, Setaria pumila,* and *Apluda mutica,* I kept a tally of the total number of phytoliths present and the number of each lobate type.

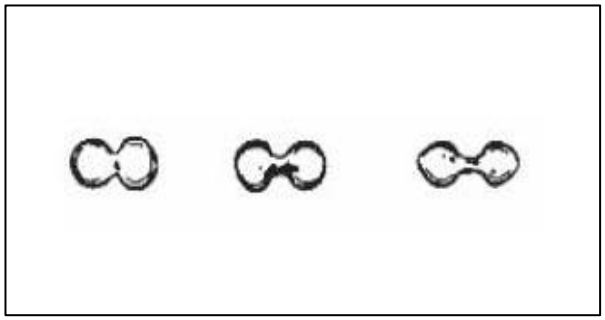

Figure 3: Bilobe Types 1, 2, and 3 (left to right) based on classifications by Lu and Liu (2003: pp. 79).

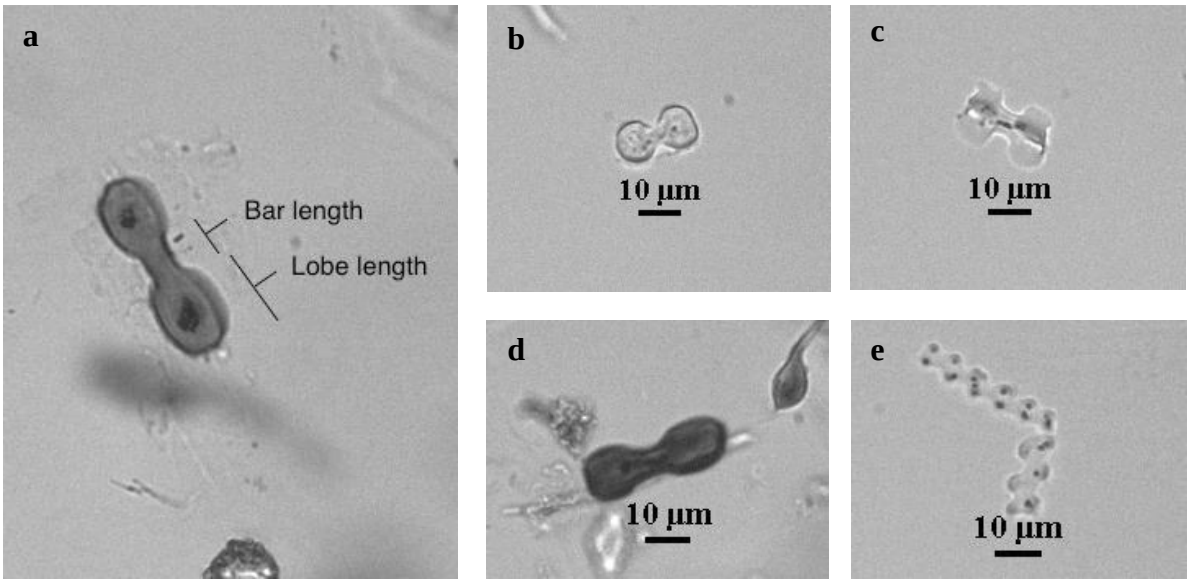

Figure 4: Lobate variation qualitatively defined by bar length (a-image from *Setaria pumila*) and classified in my study as either Type 1 (b-image from *Apluda mutica*), Type 2 (c-image from *Themeda quadrivalvis*), Type 3 (d-image from *Setaria pumila*), or polylobe (e-image from *Apluda mutica*).

Data Analysis:

To address my hypotheses, phytolith density per gram of leaf material, or acid insoluble fraction (AIF), was first calculated for each taxon and for each lobate type using the following equations (Albert and Weiner, 2001):

$$\text{Number of phytoliths per slide} = \text{Number of phytoliths counted} \times \frac{\text{Number of fields on slide}}{\text{Number of fields counted}}$$

$$\text{Phytoliths density (AIF)} = \frac{\text{Number of phytoliths per slide}}{\text{mass of phytolith weighed on slide}} \times \frac{\text{Mass of phytoliths produced}}{\text{Mass of leaf starting material}}$$

For each the three panicoid grasses, lobate ratios were calculated for easy comparison using the following equation:

$$\text{Ratio} = \frac{\text{Number per gram AIF of lobate type}}{\text{Number per gram AIF of total lobates}}$$

Two preliminary tests were then conducted to assess the validity of my results against standard principles in phytolith analysis. A Spearman's rank correlation between tier and phytolith density tested the validity of the tier classification system (i.e. whether lower-ranked taxa are associated with high levels of phytolith production). A Spearman's rank correlation between AIF and number of morphotypes was used to test the assumption that phytolith density is not related to the number of types produced (Piperno, 2006). These checks ensure that my results were not complicated by not controlling for variables such as the age of the plant, its climate history, and its precise location.

Next, Wilcoxon rank-sum tests with community as the sampling unit were used to compare AIF values [H1] and number of phytolith types [H2] between the tallgrass and inner-Nejd communities. Finally, a chi-squared test was used to test the independence of the lobate ratios [H3] for each of the panicoid grasses.

Results:

Intercommunity Analysis:

Across the ten taxa examined, phytolith morphotypes that were produced included monocot single-cells; bilobes, polylobes, cross bodies, flat towers, saddles, rondels, psilate long cells, sinuate long cells, echinate long cells, stomata, hair cells, bulliforms, ovals, trichomes, and dicot single-cells; multi-faceted polyhedrals, blocks, sheets, tracheids, and sclereids, and various multi-cells (See photos in Appendix A). In addition, five of the indicator taxa used in this study produced six morphology types that were not identifiable based on the classifications and reference materials of Southern Arabia (Fig. 5).

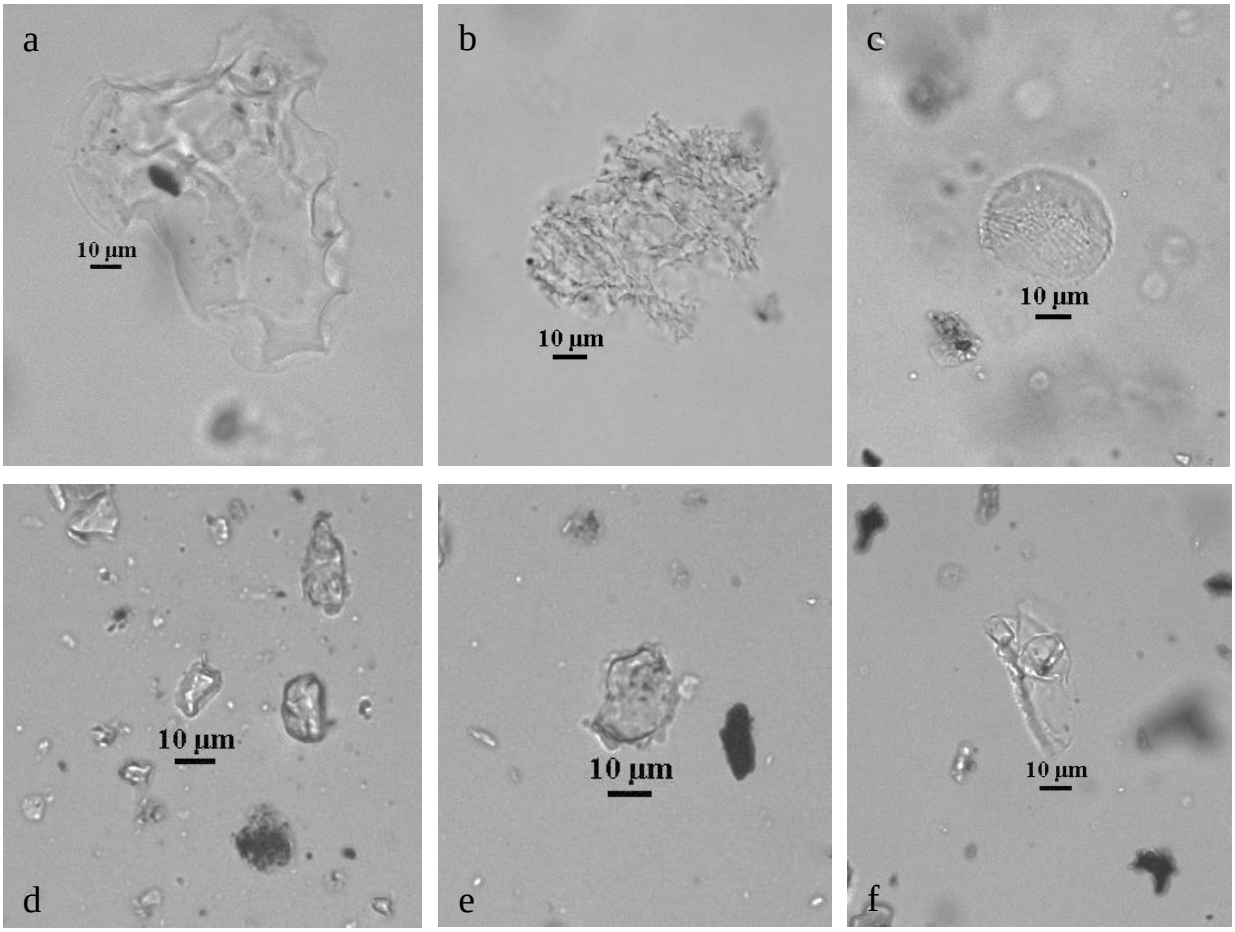

Figure 5: Unidentified phytolith morphotypes from *Commiphora gileadensis* (a), *Boswellia sacra* (b), *Abelmoschus manihot* (c), *Achyranthes aspera* (d,e), and *Euphorbia orbiculifolia* (f).

The tallgrass savannah community produced 24 phytolith types and the inner-Nejd community produced 13 types (Table 2). Eight morphotypes were found in both communities and only two types, sclereid and multi-faceted polyhedral, were found in the inner-Nejd community but not the tallgrass savannah community (Table 2). It is important to note that the bilobes, cross bodies, and trichomes found in the inner-Nejd community (Table 2) likely reflect sources of contamination because these phytolith types are produced by monocotyledons but only dicotyledons were tested in the Nejd community.

Table 2: Phytolith morphotypes found in each plant community, *likely contamination

Inner-Nejd	Morphotypes in common	Tallgrass savannah
Multi-tiered form, multifaceted polyhedral, sheet, stomata, block, tracheid, sclereid, hair cell, hair base, globular spheroid, bilobe*, cross body*, trichome*	Multi-tier form, block, globular spheroid, hair cell, hair base, tracheid, stomata, sheet	Bilobe, bilobe multi-cell, polylobe, polylobe multi-cell, saddle, cross body, tower, rondel, multi-tiered form, bulliform, oval, trichome, sheet, block, stomata, hair cell, hair base, tracheid, echinate long cell, psilate long cell, echinate multi-cell, sinuate multi-cell, psilate multi-cell, globular spheroid

There was a strong, negative correlation (Spearman's rank correlation: r=-0.6991, p=0.0245) between tier and AIF. There was a weak correlation (Spearman's rank correlation: r=4786, p=0.1617) between AIF and number of morphotypes, confirming that the two are not related. These preliminary tests validate my dataset and support evidence commonly found in phytolith literature.

Individual AIF values and the number of morphotypes found in each species are reported in Table 3. The difference in average AIF was not statistically significant between communities (Wilcoxon rank sum test: W=18.0, Z=-1.149, p=0.3095; Fig. 6). Therefore, the first hypothesis [H1] was not supported. The difference in average number of phytolith types was statistically significant between communities (Wilcoxon rank sum test: W=23, p=0.0345; Fig. 7). Therefore, the second hypothesis [H2] was supported. See Appendix B for raw data tables.

Table 3: AIF and number of phytolith types for counted taxa

Family	Taxa	Tier	Ecological Zone	AIF (phytolith/gm)	Number of types
Burseraceae	*Commiphora gileadensis*	1	Inner-Nejd	56,048	7
Burseraceae	*Boswellia sacra*	1	Inner-Nejd	20,042	11
Boraginaceae	*Trichodesma cinereum*	1	Inner-Nejd	362,107	3
Euphorbiaceae	*Euphorbia orbiculifolia*	2	Inner-Nejd	549	6
Zygophyllaceae	*Tetraena decumbens*	5	Inner-Nejd	2,032	3
Poaceae (Gramineae)	*Themeda quadrivalvis*	1	Tallgrass	66,016	12
Poaceae (Gramineae)	*Setaria pumila*	1	Tallgrass	401,105	14
Poaceae (Gramineae)	*Apluda mutica*	1	Tallgrass	257,508	14
Malvacaeae	*Abelmoschus manihot*	4	Tallgrass	16,232	11
Amaranthaceae	*Achyranthes aspera*	5	Tallgrass	22,818	7

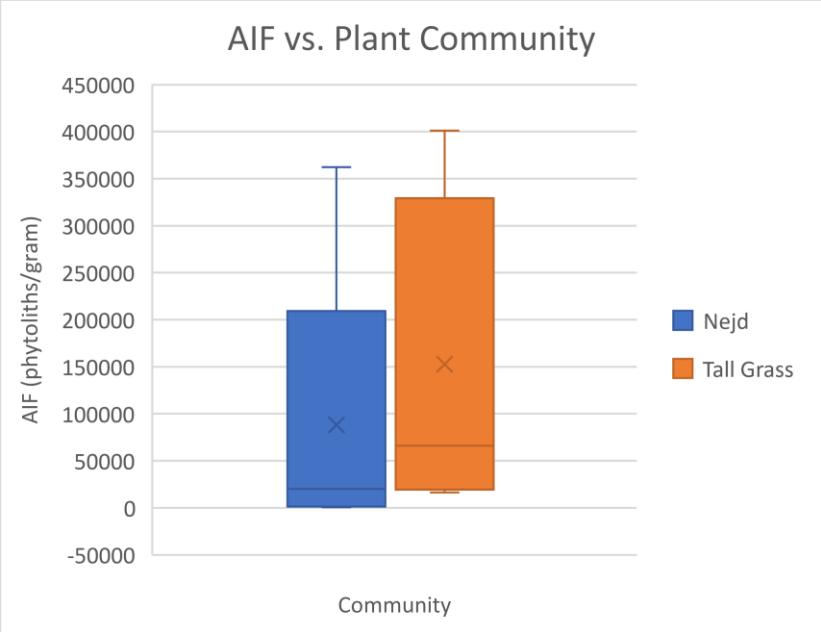

Figure 6: Descriptive statistics of average AIF values of the tallgrass and Nejd communities

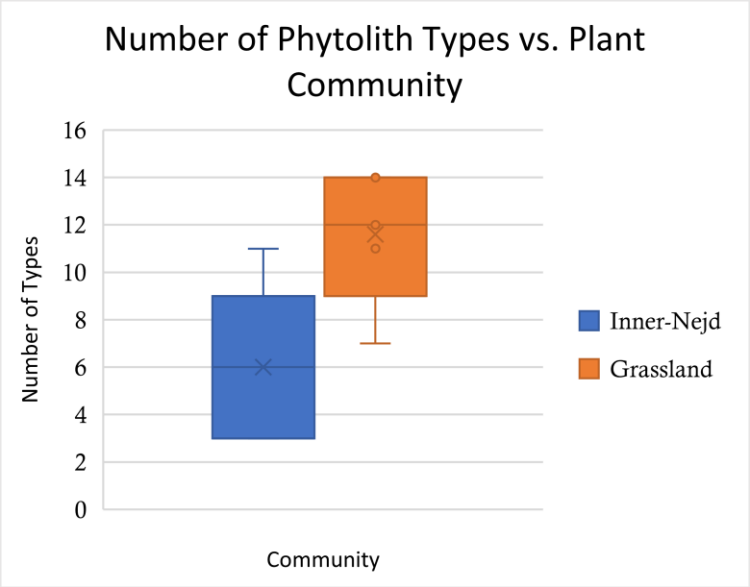

Figure 7: Descriptive statistics of number of phytolith types of the tallgrass and Nejd communities

Intracommunity Analysis of Panicoid Grasses:

The number of lobate phytoliths per gram AIF (Table 4) were used to calculate ratios by lobate type for each of the panicoid grasses (Table 5). Among the lobate phytoliths produced by *Themeda quadrivalvis*, the Type 3 bilobes had the highest ratio (0.50), followed by Type 2 bilobes, (0.28), Type 1 bilobes (0.22), and then polylobes (0.0). *Setaria pumila* also produced a high ratio of Type 3 bilobes (0.60), followed by Type 2 bilobes (0.21), Type 1 bilobes (0.12), and lastly polylobes (0.07). In *Apluda mutica*, the polylobe type was the most common of the lobate phytoliths with an abundance ratio of 0.74. Next in abundance were the Type 1 bilobes (0.16), followed by the Type 2 bilobes (0.08), and the Type 3 bilobes (0.02). I observed a significant difference in lobate ratios between the three taxa (chi-squared test: χ^2=100.15, $p<0.001$). The third hypothesis [H3] was therefore supported. See Figure 8 for an illustrative summary of the lobate ratios.

Table 4: Number of lobate phytoliths per gram AIF

	Type 1 Bilobe	Type 2 Bilobe	Type 3 Bilobe	Polylobe	Total Lobates
Themeda quadrivalvis	880	1100	1980	0	3960
Setaria pumila	10696	18718	53481	6685	89580
Apluda mutica	12017	6009	1717	55793	75536

Table 5: Ratio of lobate types for each panicoid grass

	Type 1 Bilobe	Type 2 Bilobe	Type 3 Bilobe	Polylobe
Themeda quadrivalvis	0.22	0.28	0.50	0.00
Setaria pumila	0.12	0.21	0.60	0.07
Apluda mutica	0.16	0.08	0.02	0.74

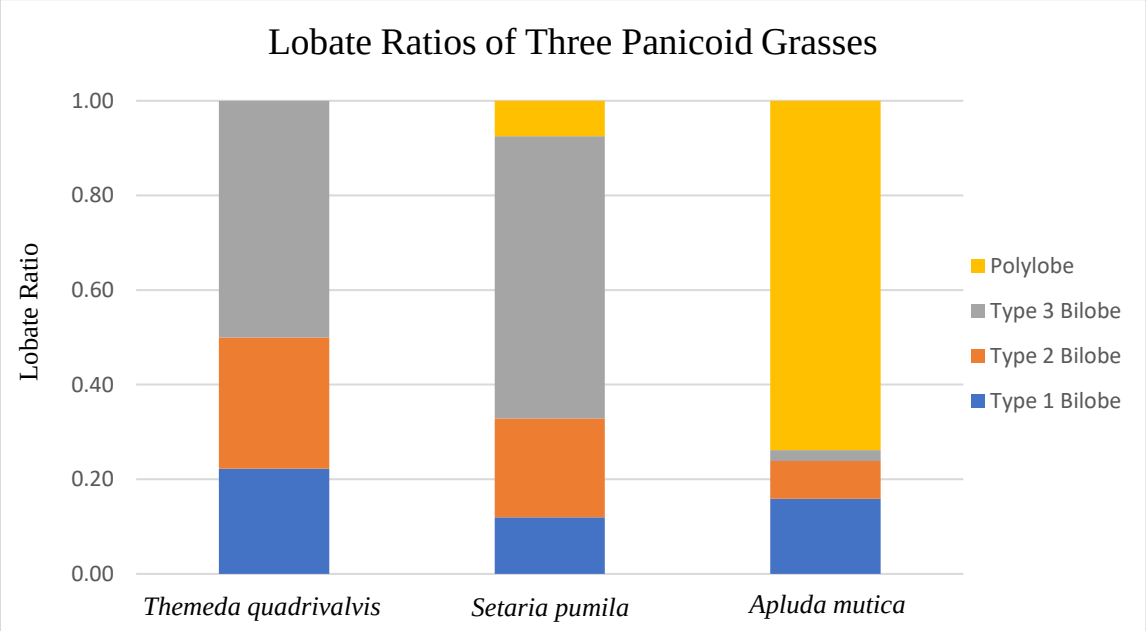

Figure 8: Lobate phytolith distributions for each of the panicoid grasses characteristic of the tallgrass savannah community.

Discussion:

Phytolith assemblages have the potential to reveal important patterns in regional vegetation dynamics and palaeoecological histories. The first step in doing so, however, is to compare phytolith densities and morphotypes from distinct vegetative reference material at the community level. In this study, the taxa of the tallgrass savannah were distinguished from the taxa of the inner-Nejd community by number of phytolith types but not by phytolith density. This finding is important because future studies could potentially develop a series of ranges for which the number of phytolith types may be indicative of a particular community. In other words, if an unknown soil assemblage produces 10-15 phytolith types it may be reflective of one defined community. An assemblage of 16-20 types might reflect another community, 21-25 types reflecting a third community, and so on. Incorporating more taxa in each community may also reveal phytolith density as a distinguishing factor, and similar range values for AIF could further be tested and defined. Interestingly, there were only two morphotypes (sclereid and multi-faceted polyhedral) that were not shared by both communities. Future work to sub-classify and quantify sclereids and multi-faceted polyhedrals may reveal that they can be used as indicator phytoliths of the inner-Nejd community.

Examination at the intracommunity level of the three grasses showed several patterns in lobate distributions. *Themeda quadrivalvis* and *Setaria pumila* were characterized by their high ratios of Type 3 bilobes with long bar lengths. Lu and Liu (2003) reported similar results for three species in the genus *Setaria* (*S. faberi, S. plicata,* and *S. palmifolia*) that were all defined by a high abundance of bilobes with longer bars. *Apluda mutica* was characterized by its high ratio of polylobe phytoliths and higher ratios of bilobes with short bar lengths compared to longer bar lengths. *Apluda mutica* was reported as a high polylobe producer in phytolith assemblages of southern China (Lu and Liu, 2003) and as one of the highest polylobe producers, along with *Themeda arundinacea,* in assemblages of West Bengal, India (Naskar and Bera, 2018). Thus, it is important to note that although the *Themeda quadrivalvis* sample in this study did not produce any polylobes, this should not be considered a diagnostic trait of the genus as a whole. It is possible that *Themeda quadrivalvis* produces small or negligible proportions of polylobes, but multiple leaf samples, as well as samples from other plant parts, should be analyzed before such conclusions are made. Nonetheless, the novel use of lobate ratios in my study allowed me to

quantify and compare the uniqueness of lobate bar lengths between the panicoid grasses. Continued development of the potential diagnostic capabilities of lobate phytoliths is important for their use as a paleoecological proxy and for understanding landscape stability and change.

Many of the results found in my dataset are consistent with other phytolith datasets from around the world, confirming the scholarly consensus that phytolith formation and general morphology is largely influenced by plant phylogeny and biology. Previous studies have examined the chemistry of silica in soils and proposed that phytoliths function to give plants mechanical support as well as defense against fungal diseases, toxins in the soil, and herbivores (Piperno *et al*., 2002; Epstein, 1994; McNaughton and Tarrants, 1983; Sangster *et al*., 2001; Iler, 1979). There have also been several studies suggesting that climate and the temperature, pH, moisture, and monosilicic acid concentration in soils may secondarily influence phytolith production (Jones and Handreck, 1965; Piperno, 1988; Rosen and Weiner, 1994; Madella *et al*., 2002; Tsartsidou *et al*. 2007). Looking specifically at grasses and bilobe phytoliths, Lu and Liu (2003) made the general observation that grasses growing in drier environments tended to form bilobes with greater bar lengths. While no scientific data currently exists to support this trend, an index ratio of bilobe types found in soil profiles could reveal patterns of increasing and decreasing bar length and paralleled shifts in aridity. Future research is necessary for determining the overall impact and to what extent environmental factors have on phytolith formation.

Despite their stability and durability in soils, there exists a potential for phytolith cross-contamination between samples particularly in a laboratory setting (Parr *et al*., 2001). Throughout the processing and extraction of our samples, extra caution is taken to ensure a clean lab space, clean equipment, and protocols aimed at minimizing contamination risk (Buffington *et al*., 2017). Nonetheless, contamination was identified in this study by encountering monocot phytoliths in dicot plant samples, such as finding a bilobe phytolith in the dicot *Boswellia sacra* slide (Fig. 9). Similarly, a cross body was found in *Euphorbia orbiculifolia* and one trichome and one bilobe were found in *Abelmoschus manihot*. Sources of contamination could include aeolian forces in the lab during weighing and mounting, cross-contamination from soils and plant parts during field collection, and general contamination of the laboratory and equipment.

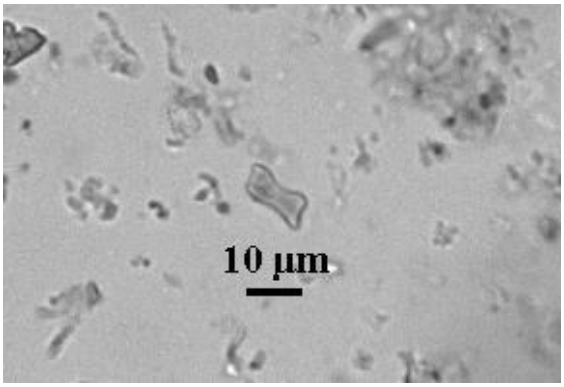

Figure 9: Evidence of contamination due to a bilobe phytolith found in the dicot *Boswellia sacra*.

There also exists a broad range of multiplicity and redundancy within phytolith analysis that limits overall diagnostic capabilities. In other words, plants of the same family and genus can produce different phytolith types (multiplicity), and plants of different families can produce the same phytolith types (redundancy). Such overlap makes it difficult to assign a specific morphotype to species or genus. Furthermore, phytolith analysis requires a high level of expertise in specialized extraction protocols and positive identification for counting, as I learned in this study. Even with such skills, the high variation in phytolith shapes and morphologies coupled with the various classification and sub-classification systems makes it difficult to correctly identify every phytolith one encounters. In this study alone, half of the analyzed species produced either an unrecognized phytolith form or a morphotype that has not been previously observed in other samples from Southern Arabia. Additional reference material and future analyses will be useful in determining whether these morphotypes are representative indicators of their corresponding taxa and plant families. Thus, I emphasize the importance of a quantitative phytolith reference collection that is specific to the highlands of Southern Arabia and to areas of archaeological significance.

Conclusion:

The goal of my study was to determine whether phytoliths could be used to distinguish between plant taxa and communities based on phytolith density [H1], number of types [H2], and lobate type ratios in panicoid grasses [H3]. Although the tallgrass and inner-Nejd plant communities did not show a significant difference in phytolith density, there was a significant

difference based on the number of types produced. Additionally, the three grass taxa demonstrated unique lobate ratios within the tallgrass savannah community. I would improve this study by expanding the number of communities and taxa analyzed. Important vegetative associations to investigate next include the *Anogeissus dhofarica* forest, the *Olea europaea-Maytenus dhofarensis* woodland, the *Euphorbia balsamifera-Commiphora foliacea* cushion shrub, and the *Launaea castanosperma-Heliotropium bacciferum* community of the exposed plateaus and wadi slopes (Patzelt, 2015). A majority of the indicator taxa that make up these communities have already been collected. Future work will consist of phytolith extractions for these species so that they may be added to our phytolith references and used for further inter- and intra-community analyses.

As shown by this study, the diagnostic capability of phytoliths is complicated by contamination and the redundancy in phytolith morphologies. Nonetheless, phytolith reference collections and community-level analyses are valuable for interpreting extracted phytolith assemblages from soil samples and reconstructing the region's vegetation history through space and time. A more complete paleoecological evaluation of Dhufar's many vegetation communities will help to better define the various ecological and transitional zones under consideration. The use of phytoliths as a proxy for differentiating between communities ultimately has important implications for assessing an ecosystem's health and resilience to overall climatic and anthropogenic influence.

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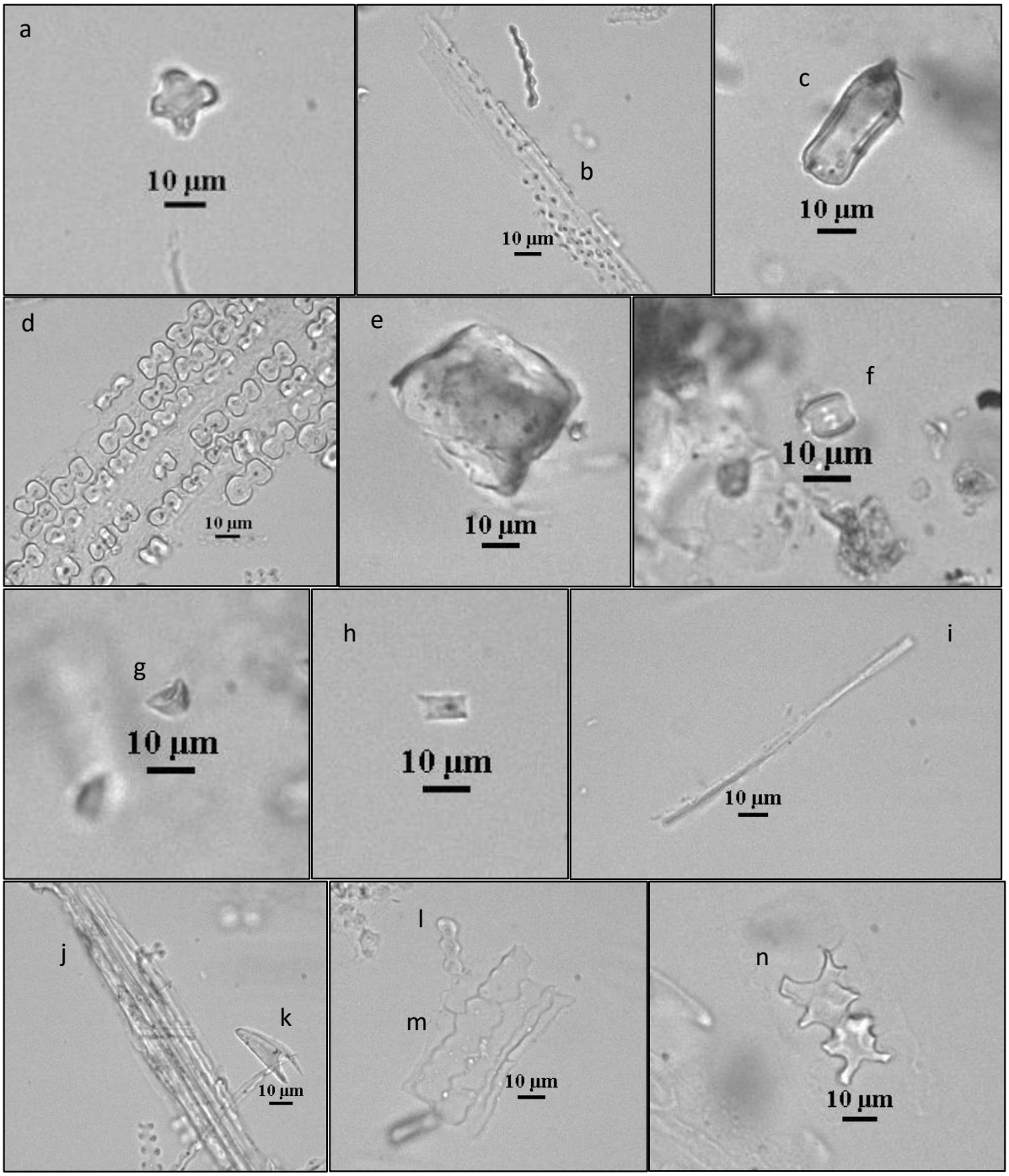
APPENDIX A: PHYTOLITH TYPE IMAGES



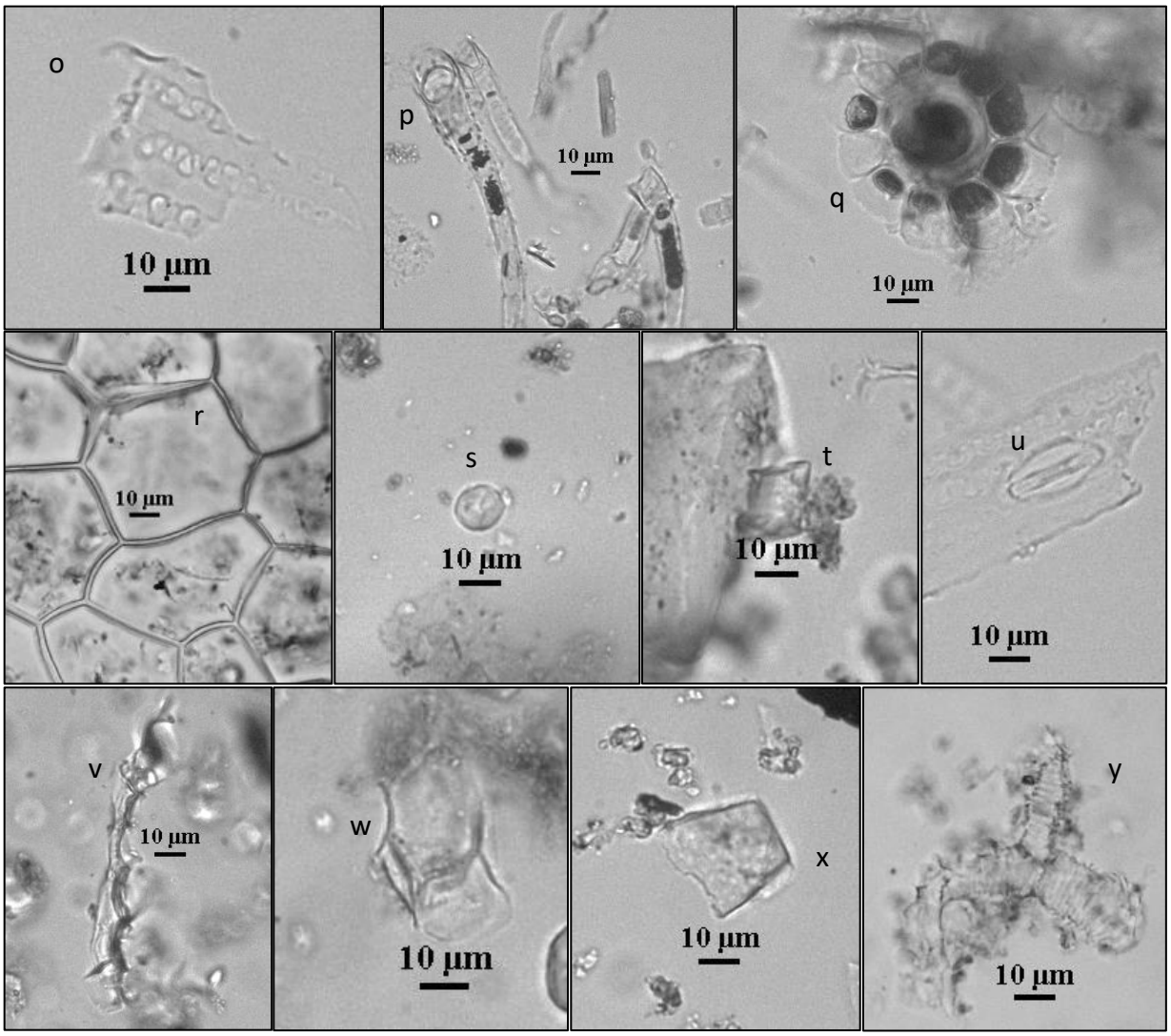


Figure A1: Images of the phytolith types identified: cross body (a), polylobe multi-cell (b), oval (c), bilobe multi-cell (d), bulliform (e), saddle (f), rondel (g), tower (h), psilate long cell (i), psilate multi-cell (j), trichome (k), polylobe (l), sinuate multi-cell (m), echinate long cell (n), echinate multi-cell (o), hair cell (p), hair base (q), multi-tiered form (r), globular spheroid (s), block (t), stomata (u) sclereid (v), multi-faceted polyhedral (w), sheet (x), tracheid (y)

APPENDIX B: RAW DATA TABLES

Table B1: Raw data to calculate total number of phytoliths per slide and number of phytoliths per gram AIF for each taxon.

	n. phytos counted	area counted (n. fields)	total area of slide (n fields possible)	n/slide	mass of phytoliths mounted on slide (mg)	mass of total phytoliths produced (mg)	mass of leaf (mg)	n. phyt. per gm AIF
Commiphora gileadensis	300	240	2304	2880	1.35	2.89	110	56048
Boswellia sacra	300	352	2304	1964	1.95	3.94	198	20042
Trichodesma cinereum	300	48	2304	14400	2	10.31	205	362107
Euphorbia orbiculifolia	48	1152	2304	96	0.21	0.24	200	549
Tetraena decumbens	34	1152	2304	68	0.4	2.63	220	2032
Themeda quadrivalvis	300	768	2304	900	0.48	3.38	96	66016
Setaria pumila	300	56	2304	12343	1.87	2.37	39	401105
Apluda mutica	300	112	2304	6171	2.35	17.65	180	257508
Albelmoschus manihot	300	304	2304	2274	1.72	2.48	202	16232
Achyranthes aspera	300	384	2304	1800	1.63	4.05	196	22818

Table B2: Raw data to calculate number of lobate phytoliths per slide and number of lobate phytoliths per gram AIF for each panicoid grass taxon of the tallgrass savannah community.

	n. phytos counted	area counted (n. fields)	total area of slide (n fields possible)	n/slide	mass of phytoliths mounted on slide (mg)	mass of total phytoliths produced (mg)	mass of leaf (mg)	n. phyt. per gm AIF
Themeda quadrivalvis								
Type 1 Bilobe	4	768	2304	12	0.48	3.38	96	880
Type 2 Bilobe	5	768	2304	15	0.48	3.38	96	1100
Type 3 Bilobe	9	768	2304	27	0.48	3.38	96	1980
Polylobe	0	768	2304	0	0.48	3.38	96	0
Setaria pumila								
Type 1 Bilobe	8	56	2304	329	1.87	2.37	39	10696
Type 2 Bilobe	14	56	2304	576	1.87	2.37	39	18718
Type 3 Bilobe	40	56	2304	1646	1.87	2.37	39	53481
Polylobe	5	56	2304	206	1.87	2.37	39	6685
Apluda mutica								
Type 1 Bilobe	14	112	2304	288	2.35	17.65	180	12017
Type 2 Bilobe	7	112	2304	144	2.35	17.65	180	6009
Type 3 Bilobe	2	112	2304	41	2.35	17.65	180	1717
Polylobe	65	112	2304	1337	2.35	17.65	180	55793